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MORPHOLOGY AND ONTOGENY OF THE SPERMOGONIA OF THE MELAMPSORACEAE

LILLIAN M. HUNTER

With plates 182–188

THE MORPHOLOGY and the ontogeny of the spermogonia of rust fungi have thus far received relatively scant attention. Contributions of greater or less significance have been made by Unger (73), Meyer (59), Tulasne (72), DeBary (29, 30), Sappin-Trouffy (66), Blackman (19), Rosen (65), Neuman (60), Maire (55), Allen (3, 5, 6, 8), Ludwig (54), Hunter (45), Jackson (47, 48) and others; but they have been so incidental, fragmentary or introductory in nature that the subject still remains largely unexplored. It would seem that such topics must be of importance with respect to spermogonia just as they are of other reproductive organs, and especially to students of systematic uredinology. Motivated by this viewpoint I have studied the spermogonia of a wide range of species. The paper here presented records part of this work. It is restricted to the Melampsoraceae, and particularly to representatives of the various genera of the Melampsoraceae that occur in temperate North America and Europe.

The material of all *Melampsora* species discussed in this paper was obtained from culture experiments made by W. P. Fraser, J. H. Faull, H. P. Bell, E. H. Moss, G. D. Darker, E. H. Bensley, W. R. Watson and the writer, and from supplementary field material, except that no naturally occurring specimens of *Melampsora Larici-Capraearum* were available.

All of the cultured material, exclusive of that obtained from Professor Fraser, was fixed when in fresh condition. Treatment of the material was similar to that described by the writer (45), with the exception that fresh material of *Uredinopsis*, *Milesia* and *Melampsora* species was sectioned by hand and studied in an aqueous solution and after mounting in lacto-phenol. A combination differential staining method, using

safranin and light green in lacto-phenol, was introduced for material of *Milesia polypodophila* and *Coleosporium* species after embedding in celloidin. This method was devised without knowledge of Lepik's (52) method of double staining in lacto-phenol. The ethyl-butyl alcohol series was preferable to the ethyl alcohol series used previous to embedding.

The data obtained on each of the species dealt with here are presented in detail with reference to (1) morphology of mature spermogonia, (2) their ontogeny. This procedure has been adopted because of the fact that detailed descriptions of these organs by other authors have been meager at best, and most frequently are non-existent. The species selected belong to the following genera and subfamilies:

I Subfamily MELAMPSOREAE — *Melampsora*
II Subfamily PUCCINIASTREAE — *Melampsoridium, Melampsorella, Pucciniastrum, Thecopsora, Calyptospora, Hyalopsora, Milesia* and *Uredinopsis.*
III Subfamily CRONARTIEAE — *Cronartium*
IV Subfamily CHRYSOMYXEAE — *Chrysomyxa*
V Subfamily COLEOSPORIEAE — *Coleosporium*

From this it will be seen that the only genera of the Melampsoraceae as recognized by Dietel under the family Melampsoraceae (Engler and Prantl's Natürliche Pflanzenfamilien, Band 6, 2nd ed. pp. 35–48, 1928) not included here are *Chnoopsora* and five genera the haploid stages of which are unknown — *Mesopsora, Phakopsora, Crossopsora, Mikronigeria* and *Bubakia.*

I. Subfamily MELAMPSOREAE

The Melampsoreae comprise three genera, namely, *Melampsora, Chnoopsora* and *Bubakia.* Three species of *Chnoopsora* are known; they occur in India and Central Africa; their spermogonia are said to be subepidermal; no material was available for study.

1. **Melampsora Abieti-Capraearum** Tubeuf

Arthur (16) considers *Melampsora Abieti-Capraearum* Tubeuf on *Abies alba* Mill. in Europe and *M. americana* Arthur on *A. balsamea* (L.) Mill. in America to be the same species. My studies on their spermogonia afford support to this conclusion.

The morphology of the spermogonia of the American rust has already been described by Hunter (45). Subsequent examination of additional specimens reveals no essentially divergent data. Quite recently my studies have been extended to the spermogonia of the European rust. The similarities of the American and the European materials

are so close that a summarized presentation of the data for both, as found in Table II below, will suffice. It should be noted, however, that in both of them certainty as to the location of mature spermogonia with reference to the epidermis is often impossible. Some are plainly subepidermal; others appear to be subcuticular. Here then is a case in which the correct description of the spermogonium requires a knowledge of its ontogeny. To clear up this point I have made a thorough study of the ontogeny of the spermogonia of this rust on *A. balsamea*, both from culture and field materials.

The spermogonial primordia in all cases examined lay immediately under and in contact with the epidermis. Usually it forms in an air space (commonly a substomatal cavity), but sometimes between the epidermis and the otherwise contiguous palisade tissue. The primordium consists essentially of closely adhering, vertical, actively growing hyphae, interpreted as spermatiophores, with a suggestion at times of a thin, basal, hyphal mat. Figure 1 (drawn from a lateral, vertical section of a mature spermogonium) adequately illustrates a typical primordium and also initial stages of disruption of overlying epidermal cells. Subsequent developmental stages comprise a thickening of the basal mat (Fig. 2) accompanied by some destruction of underlying mesophyll, and a maturing of the spermatiophores accompanied by a variable amount of destruction of overlying epidermal cells or none at all. These different effects on the epidermis, as revealed by serial sections, may occur within the limits of a single spermogonium.

Destructive action on the mesophyll is indicated in Fig. 3 by a break in the continuity of three layers of its tissues, and by the dark-staining remains of palisade cells embedded in the spermogonium. Among the epidermal cells the guard cells are the most resistant (Fig. 2). They may be invaded; but even so, their thick walls persist and the cells retain their contour. The effect on other epidermal cells is shown in Fig. 1, where it is seen that two hyphae are pushing inwards the lower wall of one cell, and others have already invaded the cell to the right the protoplasm of which is now dead. Almost all conditions of the epidermis overlying a mature spermogonium, as described above, are represented in Fig. 1 of Hunter (45).

The conclusion is that the spermogonium of *M. Abieti-Capraearum* is properly described as subepidermal, and not subcuticular as asserted by Ludwig (54). It consistently originates under the epidermis; and in the course of its development there is more or less destructive action of underlying tissues, and often of the epidermis even out close to the cuticle.

As an addendum it is of interest to note that a few sections showed long hyphae extending beyond the surface of the spermogonium. They were found centrally located in spermogonia that had just matured, never in old spermogonia. Spermatia were massed around them and, unlike paraphyses, they were ephemeral. These I interpret as the "flexuous hyphae" of Craigie (27).

2. **Caeoma Faulliana,** n. sp. O, I.

Pycnidia amphigena, inconspicua, flavida, pustulata, non immersa, hemisphaerica vel conoidea, subcuticularia, 42–145 μ lata et 27–49 μ alta, plus minusve 80 × 37 μ; pycnidiophora simplicia, non septata vel juxta bases septata, ad apicem dehiscentia, poris 12–15 × 23–30 μ. Aecidia hypophylla, maculis flavidis insidentia, secus series duas irregulares disposita, aecidiosporis globosis vel subglobosis, subtiliter verruculosis, 16–21 μ diam.

The material studied was collected by Mr. W. R. Watson on the needles of the current season of *Abies lasiocarpa* (Hook.) Nutt. at Banff, Alberta, July 8, 1925. It consisted of pieces fixed in Carnoy's fluid for study of the spermogonia and dried herbarium specimens (Herb. J. H. Faull, no. 8849). The spermogonia (Fig. 4) at once distinguish this rust from *M. Abieti-Caprаearum* which it superficially resembles. They are smaller, more elevated (pustular) and plainly subcuticular. No doubt it is a species of *Melampsora;* but until someone makes appropriate cultures the identity of its diploid phase will remain unknown. So it is tentatively referred to as a new species under the name given above.

3. **Melampsora Abietis-canadensis** (Farl.) Ludwig

The spermogonia of *Melampsora Abietis-canadensis* are borne on leaves of the current season, young cones and young twigs of *Tsuga canadensis* (L.) Carr. The affected leaves, especially those of the terminal buds, may be distorted and Adams (1) states that the same is true for affected twigs. The spermogonia are abundant, small, subcuticular, amphigenous, pustulate, and hemispherical-flattened to conoidal in vertical section (Fig. 6). The base of the spermogonium is a flat-bottomed stroma. The epidermal cells at the base of the spermogonium are separated more or less by mycelium but they are not greatly displaced; they are eventually killed and may be disrupted, though frequently their walls remain unbroken. Thirty-four spermogonia occurring on needles measured from 35–98 μ broad and 15–38 μ high, averaging 66 × 25 μ. On the cones seventy-seven spermogonia measured 53–128 μ broad and 13–30 μ high, averaging 78 × 23 μ. The spermatia are discharged through a long slit, 8–30 μ wide. The foregoing description

is based upon culture material supplied by Professor W. P. Fraser.

Considerable confusion has existed in the past with respect to the identity of *M. Abietis-canadensis* on *Tsuga* (4, 37, 38, 39, 16, 68, 69), but the conclusion as expressed by Ludwig (54) and Arthur (16) is accepted. It is pertinent, however, to call particular attention to a rust (*Caeoma dubium* Ludwig, 54) on *Tsuga heterophylla* (Raf.) Sarg. from western North America. The spermogonia of this rust are distinguished from those of *M. Abietis-canadensis* as well as from other known species of *Melampsora.* The spermogonia of *C. dubium* are subepidermal and measure 80–115 μ broad and 50–90 μ high. This affords another example of the diagnostic value of spermogonia.

4. **Melampsora Bigelowii** Thüm.

The spermogonia of *Melampsora Bigelowii* are found on needles of *Larix laricina* (Du Roi) K. Koch and *L. leptolepis* Murr. They are small, abundant, usually discrete but sometimes confluent, pustulate, amphigenous, subcuticular, and hemispherical to conoidal in vertical sections (Fig. 7). The epidermal cells below the spermogonium, except for slight separation by the mycelium, are usually left *in situ;* but occasionally they are widely separated and sometimes so completely obliterated that the spermogonium occupies the space where the epidermal cells were located, as well as extending above them. Forty-two spermogonia measured 50–102 μ broad and 15–38 μ high, averaging 69 × 27 μ. The spermatiophores may be nonseptate or one-septate towards the base. The spermatia measure 1.5–2.0 × 3–4 μ. The opening through which the spermatia are exuded is 15–30 μ wide and extends over the greater part of the spermogonium in the longitudinal direction of the leaf.

Both spermogonia and caeomata were obtained on *Larix leptolepis* and *L. laricina* from inoculation experiments in which the teliospores of North American species of *Salix* were employed. The material on *L. laricina* only was sectioned.

5. **Melampsora Medusae** Thüm.

The spermogonia of *Melampsora Medusae* occur on needles of *Larix laricina* and *L. leptolepis*. They are indistinguishable from those of *M. Bigelowii*. Both spermogonia and caeomata were obtained on *Larix leptolepis* and *L. laricina* from inoculation experiments in which teliospores from North American species of *Populus* (including *P. tremuloides*) were used. The material on *L. laricina* was sectioned.

6. **Melampsora Larici-Capraearum** Kleb.

The spermogonia of *Melampsora Larici-Capraearum* are borne on needles of *Larix laricina*. They are abundant, small, discrete or occa-

sionally confluent, pustulate, amphigenous, subcuticular and in vertical section conoidal to hemispherical (Fig. 9). The epidermis is somewhat depressed by the overlying spermogonium. Its cells are separated and sometimes killed by the hyphae which have passed through to form the basal stroma. Sometimes the area formerly occupied by these cells is filled with a mass of interwoven hyphae. Thirty-one spermogonia measured 30–101 μ broad and 18–38 μ high, averaging 65 × 28 μ. The spermatiophores may be septate towards their bases. Usually they are single-celled but they may be bicellular and the cells are uninucleate. The spermatia are catenulately produced and they measure 1.5–2.8 × 3–4 μ. The pore through which the spermatia are exuded measures 7.5 × 28.0 μ wide and may extend over the entire length of the spermogonium. Figure 8 represents an immature spermogonium. Here the cuticle may be seen stretched beyond the free ends of the spermatiophores. This condition has been observed frequently.

Spermogonia and caeomata were obtained on *Larix decidua* and *L. laricina* from the European rust in its telial stage on *Salix caprea*. The spermogonia on both species of *Larix* were studied.

II. Subfamily PUCCINIASTREAE

7. **Melampsoridium betulinum** (Pers.) Kleb.

The spermogonia of *Melampsoridium betulinum* occur on needles of *Larix decidua*. They are abundant, minute, amphigenous, subcuticular, pustulate and in vertical section hemispherical flattened to conoidal (Fig. 5). The epidermal cells may remain *in situ* or may be separated by mycelium. The spermogonia measured 45–53 μ broad and 12–15 μ high. The spermatiophores arise from a stroma which forms over the epidermal cells. The opening through which the spermatia are emitted is a slit 8–11 μ wide. The spermogonium of *M. betulinum* is of the same type as that of *Pucciniastrum* species and of such species of *Melampsora* as *M. Bigelowii* and *M. Medusae*.

Arthur (15) reports the haploid stage on *Larix laricina* (Du Roi) Koch from Connecticut and Wisconsin. An examination of specimens from the materials on which the American records are based (supplied through the courtesy of Dr. G. P. Clinton) shows the rust is *Melampsora* sp. True, a few weak peridial cells are present in the aecia but nowhere is there any indication of a well-defined peridium. Since it is now known that fragile, evanescent peridia are present in certain *Melampsora* species, this may account for the confusion which has resulted in error in determination. So far then as verified records go, the haploid stage of *Melampsoridium betulinum* has yet to be found in North America.

In 1898 Klebahn (51) established the genus *Melampsoridium*. He successfully cultured the rust on *Larix* and identified the haploid stage (bearing typical peridermia) with the *Caeoma Laricis* of Plowright (63). The writer has cultured from the telial stage of *M. betulinum* (from *Betula verrucosa*) to *Larix decidua* and *L. laricina*, obtaining scanty infection of both spermogonia and aecia. The latter are true peridermia.

8. **Melampsorella Cerastii** (Pers.) Schroet.

A description of the morphology and of the ontogeny of the spermogonium of *Melampsorella Cerastii* is already recorded by the writer (45) under the name *Melampsorella Caryophyllacearum*. Figure 10 adds an excellent photographic illustration.

9. **Pucciniastrum Epilobii** (Pers.) Otth.

10. **Pucciniastrum Abieti-Chamaenerii** Kleb.

The spermogonia of one of these species, the identity of which was unknown at the time, has already been described by the writer (45) under the name *P. Epilobii*. Subsequently, authentic culture materials of both were made available through the courtesy of Professor Faull, and their spermogonia have been studied in detail. No constant differences were evident. Professor Faull, however, pointed out that there are specific differences in the aecia of the two species, and my examination of his herbarium specimens leads me to the same conclusion.

11. **Pucciniastrum americanum** (Farl.) Arth.

The spermogonia of *Pucciniastrum americanum* occur on leaves of the current season of *Picea glauca* (Moench) Voss. They are small, discrete, amphigenous, irregularly scattered, subcuticular, pustulate, and in vertical section hemispherical flattened in shape. The epidermal cells at the base of the spermogonium are separated by hyphae passing between them into the spermogonium. As the rust nears maturity these cells are somewhat depressed and frequently die; but there is no great disruption of host tissue. Twenty-nine spermogonia were found to measure 71–185 μ broad and 18–62 μ high, averaging 124 × 35 μ.

The spermatiophores are usually either nonseptate or one- to two-septate in the lower third of their length. They branch, just as do those of *P. arcticum* (Fig. 13), from enlarged basal hyphae. The spermatia form catenulately and they measure 1.5 × 3.5 μ in my sections. Measurements of spermatia from fresh material according to Darker (28) are 2.0–2.4 × 3.9–5.9 μ. Frequently the opening through which the spermatia emerge measures 7.5–45.0 μ broad and extends as a slit over the greater part of the spermogonium. The cuticle may curl back exposing a considerable area of the upper surface of the spermogonium. At ma-

turity "flexuous hyphae" have been found extending beyond the tips of the spermatiophores through the opening of the spermogonium.

12. **Pucciniastrum arcticum** (Lagerh.) Tranz.

The spermogonia of *Pucciniastrum arcticum* occur on first year needles of *Picea glauca* and resemble those of *Pucciniastrum americanum* so closely that it is probably impossible to separate them on a morphological basis (Fig. 12). It should be noted, however, that the spermatiophores of *P. arcticum* are commonly one-septate near their bases (Fig. 13). The spermatia, too, are possibly distinctive. In prepared sections they were found to measure 1.5–3.0 × 4.5–6.0 μ. Darker's measurements (28) made from fresh material were 1.3–1.6 × 3.9–4.7 μ.

13. **Thecopsora minima** (Schw.) Syd.

The spermogonia of *Thecopsora minima* are borne on the leaves and young cones of *Tsuga canadensis*. Spermogonia on the leaves only were examined by the writer. They are small, usually discrete but occasionally confluent, amphigenous, irregularly scattered over the leaf surface, subcuticular, pustulate and in vertical section conoidal to hemispherical flattened. Thirty-four spermogonia measured 38–120 μ broad and 15–25 μ high, averaging 79 × 20 μ. The opening through which the spermatia are exuded measures 14–15 μ wide and extends as a slit over the spermogonium for most of its length. The materials studied were obtained from Professor W. P. Fraser. He secured them by inoculating *Tsuga canadensis* with basidiospores from *Rhodora canadensis*.

A difference of opinion exists (37, 16, 38, 39, 64, 1, 70) as to whether or not *T. minima* and *T. Myrtilli* are distinct species. It is doubtful if the spermogonial characters afford any aid in answering this question. It should be added that in all of the experimental work carried on in connection with *Thecopsora minima* and *T. Myrtilli* the infection experiments necessary to prove that the uredial stage on the various telial hosts *Vaccinium, Gaylussacia, Rhodora* and *Azalea* have never been performed. Gross inoculations with urediospores from one diploid host plant to the other would be of some value; but the experiments should be carried on by inoculating from the telial stages on various hosts to *Tsuga,* and when the aecia are secured inoculations should be made from each source back to all the various telial hosts. It would be well to include *Thecopsora Hydrangeae* in such a set of experiments.

14. **Thecopsora Myrtilli** (Schum.), n. comb.

Aecidium ? Myrtilli Schum.

My study of the spermogonia of *Thecopsora Myrtilli* is based on culture material obtained by Fraser (38) as the result of inoculations from

Vaccinium canadense Kalm on to *Tsuga canadensis* (L.) Carr. No significant differences were found between those of *T. Myrtilli* (Fig. 14) and *T. minima*.

15. **Thecopsora Hydrangeae** (B. & C.) Magn.

The spermogonia of *Thecopsora Hydrangeae* are borne on first year needles of *Tsuga canadensis*. They are small, usually discrete but sometimes confluent, amphigenous, subcuticular, pustulate and in vertical section hemispherical flattened to low conoidal. The stroma of the spermogonium does not usually depress the underlying epidermal cells. Thirty-five spermogonia measured 75–126 μ broad and 15–26 μ high, averaging 99 × ·24 μ. The aperture through which the spermatia are discharged is a slit 15–23 μ wide.

16. **Calyptospora Goeppertiana** Kühn

Since an earlier study of the spermogonia of this rust was made by the writer (45) examination of another lot of cultured material confirms the fact that spermatia do not ordinarily form and that the cuticle above the spermogonium remains unbroken. More than five hundred spermogonia have been examined. In these, spermatia were never found to have emerged. In many of the sections mature aecia were present. Frequently the spermogonia are dwarfed. Occasionally growth proceeds little further than is shown in Fig. 11.

17. **Hyalopsora Aspidiotus** (Pk.) P. Magn.

The morphology of the spermogonia of *Hyalopsora Aspidiotus* has already been adequately described (45) and due reference made to Mayor's findings in European material (57). Recently Kamei (50) has described similar but apparently somewhat bulkier spermogonia of his new species *H. aculeata*, cultured by him from *Blechnum Spicant* var. *nipponicum* (K.) M. & K. to *Abies Mayriana* Miy. & Kudo. In continuation of my studies on *H. Aspidiotus* on *Abies balsamea* I am now able to present for the first time an account of the ontogeny of its spermogonia.

The young spermogonium arises subepidermally from a very loosely scattered weft of mycelium in the outer intercellular spaces of the mesophyll (Fig. 16). At a very early stage in its development, hyphae (potential spermatiophores) branch off anticlinally from this weft; and very soon they come to form a continuous layer directly under the epidermis. During the latter process the intervening mesophyll cells are loosened from their connection with the epidermis and they and their neighbors in the outer layer of mesophyll are pressed downward into the spaces below. Frequently a number of the mesophyll cells become in-

volved in the growth of the spermatiophores. They are surrounded and eventually disrupted (Fig. 15). At maturity the epidermal cells above the spermogonium are usually killed; occasionally their walls are broken down by the mycelium (Fig. 16); and at times they may be penetrated by haustoria (Fig. 16). During the formation of the spermogonium the host leaf tissue becomes much swollen (Fig. 15) and drops of tannin and resinous matters form in affected cells — the former being especially abundant in the immediate neighborhood of the spermogonium. Within this region, too, starch grains fill the cells in abnormal amounts.

18. **Milesia intermedia** Faull

In an earlier paper the mature spermogonium of *Milesia intermedia* on *Abies balsamea* was described by the writer (45) under the name *Milesina Kriegeriana* Magnus. Faull (35) has recently shown that the latter is a different species and that it is not known to occur in America. The spermogonia of *M. intermedia,* just as is true of other known Milesian spermogonia, are depressed in the host tissues at maturity. But an examination of mature spermogonia of *M. intermedia,* just as with most species of *Milesia,* leaves one in doubt as to their relation to the epidermis, that is, as to whether they are subepidermal, intraepidermal or subcuticular. To arrive at the correct interpretation in such species ontogenetic studies are necessary. These have been made for several of them by the writer. An account of the ontogeny of the spermogonium of *M. intermedia* follows. It plainly is of subcuticular origin.

The spermogonium of *Milesia intermedia* (Fig. 17) originates in the outer epidermal wall. Hyphae separate the granular layer underlying the cuticle from the wall strata below and growth of the young spermogonium continues in that region. As growth progresses the cuticular and granular strata are elevated and the underlying epidermal cells are depressed.

The formation of the pore in the cuticle, through which later the spermatia are exuded, is of interest. A spermogonium about half developed is shown in Fig. 18. At a central point above the row of spermatiophores, the granular stratum which normally occurs immediately below the cuticle has disappeared. It is at this point that the cuticle breaks, the rupture being caused by pressure exerted by lateral growth of the fungus, and also by the filling of the cavity in the spermogonium with spermatia and spermatial fluid.

At this intermediate stage (Fig. 18) in the growth of the spermogonium the spermatia are well developed. The spermatiophores are fewer and much more separated than in the mature stage. The growth of the spermatiophores is from the stroma. They increase in number by

branching from the cells of the stroma. As the spermatiophores multiply the underlying epidermal cells are pressed more deeply into the host tissue and some of them completely disintegrate.

The mature spermogonium, which, in an early phase was raised and lenticular, is approximately plane with the leaf surface on its outer facies. Its body is hemispherical and deeply immersed as the result of prolific basal growth.

19. **Milesia fructuosa** Faull

Milesia fructuosa was produced in Faull's (36) cultures on various species of *Abies* (Table I), and always on leaves of the first season. In these experiments the rust developed scantily on *A. nephrolepis* Maxim., *A. amabilis* (Dougl.) Forbes and *A. balsamea* and sometimes only spermogonia were borne; on *A. concolor* Lindl. & Gord. the rust was more abundant; but on *A. magnifica* Murr., *A. Fraseri* (Pursh) Lindl. and *A. Fraseri prostrata* Rehd. it was not only abundant but it distorted the leaves of the host. The distorting effect was very marked on *A. magnifica*. The writer studied the spermogonia obtained in these cultures; the results are recorded in Table I.

TABLE I.

Fir host	Number of spermogonia measured	Range in size Breadth × Height in μ	Average size Breadth × Height in μ	Remarks
A. amabilis	8	100–180 × 68–84	134 × 70	Mostly hypophyllous
A. balsamea	17	112–140 × 76–96	137 × 81	Mostly hypophyllous
A. cephalonica	—	Dead areas only	———	
A. concolor	32	80–160 × 52–92	121 × 67	Mostly hypophyllous
A. Fraseri	64	72–152 × 40–100	117 × 76	Mostly hypophyllous
A. Fraseri prostrata	68	88–144 × 40–100	116 × 68	Mostly hypophyllous
A. magnifica	198	80–172 × 48–96	121 × 60	Amphigenous
A. nephrolepsis	6	108–180 × 40–80	132 × 66	Mostly hypophyllous

It will be noted that the measurements for the spermogonia of *M. fructuosa* vary somewhat from those given for *M. intermedia;* yet, if the mean or average measurements of the former are considered, they closely approach those given for the latter. Partly for this reason Faull (36) is inclined to regard these two as the same species (*M. fructuosa*). Certainly their spermogonia are, in general, similar in form and measure-

ments; and both are of subcuticular origin. The greatest aberration was found on *Abies magnifica* — on that host three percent of the spermogonia proved to be subpustulate.

20. **Milesia marginalis** Faull & Watson

The spermogonia of *Milesia marginalis* have been described by Hunter (45), Faull (35) and Arthur (16) as being subcuticular; and that is what mature spermogonia, with very rare exceptions, appear to be. But a study of their ontogeny shows that they originate subepidermally; and then, as development proceeds, by partially breaking down the covering epidermal cells from below, they come to lie in a subcuticular position much as though they had originated directly under the cuticle. Stages shown in this interesting sequence are represented in Figs. 19–21; and the condition at maturity is illustrated in Fig. 23 of this paper and Fig. 10 of an earlier paper by the writer (45).

Figure 19 portrays a spermogonial primordium — a thin mat of hyphae that is separating the epidermis from the underlying layer of mesophyll cells. On its outer facies it has projected haustoria into the epidermal cells and has already begun disintegration of epidermal cellular contents and lower cell walls. Indeed, hyphae now completely occupy a median epidermal cell shown and press against the inner face of its outer wall. The central part of the pad has forced the underlying mesophyll cells downward — the beginning of a process that terminates in a deeply depressed type of spermogonium.

Figure 20 represents a later stage, but a still very young condition of a spermogonium. The spermatiophoric layer is now clearly defined; destructive action from below outwards on the epidermis is proceeding apace; and the depression of the spermogonium into the mesophyll is much more marked.

Figure 21 is drawn from a more advanced stage of an immature spermogonium. All that now remains of the overlying epidermal cells are the cuticle, outer strata of the superior walls and tooth-like portions based on them of the anticlinal partitions. Depression of the basal stroma is continuing, but the final hemispheric form has not yet been attained. Perhaps the most striking new feature is the space now lying between the spermatiophoric layer and the reduced epidermal covering. This is the beginning of a hemispherical, fluid-filled cavity seen in a typical mature spermogonium. As yet spermatia are not forming but migrations of nuclei into the tips of a few of the spermatiophores and appearances of subterminal constrictions indicate that the first spermatia are being organized.

Figure 23 (cf. Hunter, 45) is a good photomicrograph of a section

through a mature spermogonium. Spermatia are being produced abundantly and the central space is doubtless filled with spermatial fluid. The position of the slit through which the spermatia are discharged is evident. It is of particular interest to note that the epidermal membrane consists of the cuticle and a dark-staining layer (the middle of the outer epidermal wall). On the latter are based projections representing middle lamellar substance of the anticlinal partitions.

In conclusion two observations are worthy of record. (1) Very occasionally the overlying epidermis may remain partially (Fig. 22) or wholly intact. (2) A central core of hyphae much longer than spermatiophores has been seen in spermogonia that have reached about three-quarters of their full size. These are interpreted as being "flexuous hyphae," that is, hyphae which possibly are receptive organs with respect to the phenomenon of fertilization.

21. **Milesia polypodophila** (Bell) Faull

The morphology of the spermogonium of *Milesia polypodophila* (Fig. 26) has already been described by Hunter (45). Its ontogeny has not been studied, but note should be made of the fact that "flexuous hyphae" are present at the time the spermogonium has matured (Fig. 24).

22. **Milesia Blechni** (Syd.) Arthur

The spermogonia of *Milesia Blechni* occur on leaves of the current season of *Abies alba* (Fig. 30) and *A. cephalonica* Loud. They are amphigenous but usually hypophyllous, immersed and more or less flask-shaped in vertical sectional view. Nine spermogonia measured 110–175 μ broad and 105–150 μ high. In the absence of ontogenetical studies it is not possible to decide definitely whether they are of subcuticular or subepidermal origin.

23. **Milesia Kriegeriana** (Magnus) Arthur

The spermogonia of *Milesia Kriegeriana* are borne on leaves of the current season of *Abies alba, A concolor* and *A. grandis* Lindl. They are inconspicuous, colorless, abundant, amphigenous, irregularly scattered, subcuticular, immersed, extending well into the mesophyll and hemispherical in sectional view (Fig. 31). No discoloration of the leaf or presence of any lesion can be detected with a hand lens until the spermogonia reach maturity, that is, at the time the spermatial fluid begins to be exuded. Then the affected areas become slightly lighter in color and of a pale yellowish tint. Sixteen spermogonia measured 98–168 μ broad and 94–168 μ high, averaging 129 × 126 μ. The spermatiophores are septate at a distance of about one-third of their length from the base of the spermogonium. They are rarely two-septate. The

cells are uninucleate. The spermatia are catenulate, hyaline and narrowly cylindrical, measuring 1.5–2.0 × 3.5–5.0 μ. They are exuded through a slit-like pore measuring 7.5–15.0 × 25–80 μ. It should be added that while the spermogonia of *M. Kriegeriana* on *A. alba* and *A. grandis* are identical, those on *A. concolor* are shallower on the average.

Mayor (58) describes the spermogonia of *M. Kriegeriana* on *A. alba* as small, rounded, immersed in the tissues and 34–42 μ in diameter — a description so different from that of the writer's that the question arises as to the identity of Mayor's materials.

My studies on the ontogeny of the spermogonia of *M. Kriegeriana* demonstrate their subcuticular origin. Previous to the formation of the young spermogonium, hyphae separate the epidermal cells laterally and then extend periclinally within the outer walls of the epidermal cells. The lateral extensions lie in a plane just below the intermediate wall stratum. Before long the epidermal cells appear to be surrounded by mycelium. The primordial stroma of the spermogonium originates, however, from the layer of mycelium in the outer epidermal wall. Young spermatiophores are formed anticlinally on this stroma. The cuticle is raised above the surrounding leaf surface as in *M. intermedia*. After this stage is reached, basal growth of the spermogonium takes place rapidly. The epidermal cells are depressed and eventually disrupted. The basal stroma expands, the spermatiophores increase in number and the spermogonium as a whole begins to take on a hemispherical form. These processes, accompanied by flattening or destruction of contiguous mesophyll cells, continue until maturity is reached. The eventual form of the spermogonium is very similar to that of *M. intermedia*.

24. **Milesia Polypodii** White

The spermogonia of *Milesia Polypodii* are borne on leaves of the current season of *Abies alba* and *A. concolor*. They are inconspicuous, abundant, amphigenous, subcuticular, colorless, immersed in the mesophyll, in vertical section hemispherical to slightly flask-shaped. No lesion or discoloration of the leaf is present until very shortly before the spermogonia open; then the affected areas become slightly lighter in color and of a pale yellowish tint. Thirty-four spermogonia measured 120–228 μ broad and 105–194 μ high, averaging 177 × 162 μ. They are usually broader than high. The spermatiophores are frequently septate at about one-third of their length from the basal stroma. They may be non-septate or two-septate. The spermatia are narrowly cylindrical, hyaline, catenulate, and measure 1.5–2.0 × 4–5 μ.

Although many of the spermogonia on *Abies concolor* were deeply immersed and reached a size almost as great as those on *A. alba*,

nevertheless, they were frequently found to be raised somewhat above the surrounding epidermis and in such instances were much shallower than the immersed type on *A. alba*. *Milesia Polypodii* on *A. concolor* caused much distortion of the leaves, whereas on *A. alba* there was no noticeable distortion except that the leaf was distended where spermogonia were present. In both hosts the mesophyll cells of the region in which they occur are destroyed in the course of development.

The ontogeny of the spermogonia of *M. Polypodii* was studied from culture materials on *Abies concolor* and *A. alba*. They form essentially in the same way as those of *M. Kriegeriana*. Swollen hyphae separate the mesophyll cells immediately underlying the epidermal cells, and these are also separated laterally from one another by strands of mycelium. Eventually a mat of hyphae, by growth in a periclinal direction, cleaves the outer epidermal cell walls, thus coming to lie just below the layer that consists of the cuticle and the granular stratum. It is mainly from the mat developed in this location that the spermogonium originates. On the upper facies of the mat spermatiophores grow out towards the cuticular covering and the isolated epidermal cells are irregularly distributed near its base. This stage is illustrated in Fig. 25, taken from a spermogonium about one-third grown. When the spermogonium has reached from one-half to two-thirds of its mature size (Fig. 32) a very interesting morphological phenomenon is to be observed. The spermatiophores, not yet fully grown and not sporulating, are present in a semi-circular ring; while much longer, broader, non-tapering, non-septate, uninucleate hyphae, apparently rising from the same stroma as the spermatiophores, form a central core. The spermatiophores stain very deeply in contrast with the hyphae of this core. At an earlier stage in development than that just described, the central core of hyphae may be in contact with the overlying membrane of the host; but it soon becomes separated and when the "slit" is formed the hyphae of the core emerge and grow out 20 μ or more beyond the covering of the spermogonium. Sections of nearly mature spermogonia in which the spermatia have formed, but in which the cuticle is not yet ruptured, show that the spermatia have no particular tendency to cling to the long hyphae; but once the spermogonium has ruptured and there has been opportunity for contact with spermatia from other spermogonia the long hyphae may be found with spermatia attached. The dark band lying over the spermogonium shown in Fig. 33 is made up of spermatia apparently massed around the long hyphae. Occasionally a hypha is seen protruding from among the exuded spermatia and sometimes one can be recognized when cut transversely in section. Just what these long

hyphae are is not certain, but according to my interpretation they are "flexuous hyphae" as described by Craigie (27) for certain Pucciniaceae.

25. **Milesia Scolopendrii** (Fuckel) Arthur

The spermogonia of *Milesia Scolopendrii* are borne on leaves of the current season of *Abies alba* and *A. concolor*. They are inconspicuous, amphigenous, apparently subcuticular, colorless, immersed in the mesophyll, in vertical section conspicuous and hemispherical to slightly flask-shaped. Twenty-eight spermogonia measured 120–228 μ broad and 100–188 μ high, averaging 156 × 140 μ. These measurements are within close range of those given for *M. Polypodii* and it is difficult to distinguish these rusts by their spermogonia. The spermatiophores are usually one- or two-septate near their bases; but occasionally they are entire. The spermatia are catenulate, hyaline, narrowly cylindrical, 1.5–2.0 × 4–5 μ. The opening through which they are exuded measures 5–38 × 40–110 μ.

No early stages in the development of the spermogonia were studied. But interesting observations were made on "flexuous hyphae" in mature or submature spermogonia. Spermogonia, twenty-seven to thirty days following inoculation on *Abies alba* and from which spermatia were just beginning to discharge, contained unusually long "flexuous hyphae" protruding far beyond the apical "slit." Hand sections of fresh material were made, then mounted in water, and finally preserved in lactophenol tinted lightly with acid fuchsin stain. Some of the "flexuous hyphae" in these sections were turgid and filled with cytoplasm, while others appeared empty and flaccid. One section was of especial interest (Figs. 28, 29). In it the spermatiophores were of normal length and spermatia were present; but standing out in the central cavity there was a long flexuous hypha with spermatia attached, extending slightly beyond the aperture and about 105 μ beyond the tips of the spermatiophores (Fig. 27). Another hypha was present to which spermatia were also attached, and these, as in the former instance, had remained adherent throughout the processes of washing and staining. In this same section there were at least six other "flexuous hyphae" in various conditions of turgidity or flaccidity. It may be added that "flexuous hyphae" were never found in old spermogonia. While the writer is not prepared to venture an opinion on the part played, if any, by "flexuous hyphae" in the sexual phenomena of rusts, yet, in continuation of such studies as have been made on this topic by Craigie (24–27), Pierson (62), Andrus (10) and Allen (7–9) it is suggested that species of *Milesia* would appear to afford excellent material. Their spermogonia are relatively large, they lack confusing paraphyses and they produce striking "flexuous hyphae."

26. **Milesia vogesiaca** (Sydow) Faull

The spermogonia of *Milesia vogesiaca* (Fig. 34) occur on leaves of the current season of *Abies alba*. They are inconspicuous, very abundant, amphigenous but mostly epiphyllous, apparently subcuticular, plane on the upper surface, deeply immersed in the mesophyll, and in vertical section spherical to slightly flask-shaped. Thirty-four spermogonia measured 154–241 μ broad and 168–214 μ high, averaging 201 × 195 μ. The spermatiophores branch from enlarged hyphal cells of the stroma which forms the base of the spermogonium. They are usually one-septate towards their bases but they may be two-septate, the second septum being about one-third of the length of the spermatiophore from its base. The spermatia are narrowly cylindrical, hyaline, 1.5–2.0 × 4–5 μ. The opening through which they are exuded is a slit-like pore in the cuticle, 5–35 × 30–70 μ. "Flexuous hyphae," 6–9 μ in diameter, occur in mature or submature spermogonia.

The spermogonia of *M. vogesiaca* are much larger than those of any of the other European species of *Milesia*. They more nearly approach those of *M. polypodophila* in size, although the latter are generally larger. The spermogonia of *M. polypodophila* are subspherical, being elongated slightly along the vertical axis; while those of *M. vogesiaca*, also subspherical, are most frequently slightly elongated along the horizontal axis. Moreover, the spermogonia of *M. polypodophila* are distinctly subepidermal and also differ from those of *M. vogesiaca* in their much longer incubation period. Confusion as to the position of the latter in the host may result because the subcuticular area above the spermogonium is so narrow that in a lateral section there is an appearance of being subepidermal. Ontogenetic studies alone can determine whether or not the spermogonia are really of subcuticular origin.

27. **Peridermium rugosum** H. S. Jackson

The morphology of *Peridermium rugosum* was described by the author in an earlier paper (45).

28. **Uredinopsis mirabilis** (Peck) Magnus

The spermogonia of *Uredinopsis mirabilis* occur in *Abies balsamea* on leaves of the current season. They are inconspicuous, rarely confluent, hypophyllous, subcuticular, colorless, immersed in the mesophyll, in vertical section hemispherical and either quite flat on top, slightly raised above the surrounding epidermis or, in late maturity, centrally depressed. Forty-nine spermogonia measured 58–123 μ broad and 35–54 μ high, averaging 89 × 44 μ. The same condition which exists in *Milesia intermedia* is found in *U. mirabilis*, namely, the combined cuticle and

the intermediate wall layer remain over the spermogonium at maturity. The spermatiophores are one-septate, or occasionally two-septate, towards their bases. The basal cells are long and tubular, narrowing toward their upper ends. Formerly (45) this was thought to be an aid in distinguishing *Uredinopsis* species from *Milesia* species; but equally large basal tubular cells have since been found in the spermatiophores of *Milesia* species. The spermatia are oval, hyaline, catenulate and measure 1.5–2.0 × 3.5–4.2 μ. The opening in the cuticle through which they are exuded is a pore or short slit, 4–9 × 10–40 μ.

Doubt has existed as to whether the spermogonia of this and various other species of *Uredinopsis* are subcuticular or subepidermal. Thus Arthur (15), in referring to the mature spermogonia of *Uredinopsis*, speaks of them as "extending between and depressing the tissues beneath, giving the appearance of being subepidermal." Indeed, it seems from the mature spermogonia as if this might be the case; but investigations of the earlier phases of their development in *U. mirabilis* show them to arise in a subcuticular fashion. After a certain amount of growth, the haploid mycelium begins to be directed towards the leaf surface and passes between the cells, along the middle lamellae, occasionally completely separating the epidermal cells from one another. Then the hyphae grow laterally and separate the outer epidermal wall into two layers. There is an interweaving of these hyphae and a stroma is organized; simultaneously, branches of mycelium from the stroma are sent out anticlinally and gradually the cuticle is raised. At the same time the underlying epidermal cells are slightly depressed due to pressure from the growth of the developing spermogonium. Figure 35 is an illustration of an early stage in the development of the spermogonium. It shows that the epidermal cells at the base have been separated and at least partly surrounded by the mycelium.

Although in its very early stages the spermogonium is superficial and raised above the epidermis, it later becomes immersed in the leaf tissue. The young spermatiophores increase in number and lengthen. The epidermal cells gradually become crushed and finally they may disappear entirely. Usually the mesophyll cells immediately underlying the spermogonium are pushed downward into the leaf, probably filling up an intercellular space; occasionally they may be involved in the growth of the stroma and disappear. As the spermogonium becomes immersed the overlying cuticle resumes its former position and is more or less on a level with that covering the surrounding epidermis.

29. **Uredinopsis Atkinsonii** Magn. (Fig. 36)

30. **Uredinopsis Osmundae** Magn.

31. **Uredinopsis Phegopteridis** Arthur

32. **Uredinopsis Struthiopteridis** Störmer

The spermogonia of all the four preceding species except *Uredinopsis Struthiopteridis,* have already been described by the writer (45). All resemble those of *U. mirabilis* so closely that these species cannot be distinguished from one another by their spermogonia. A recapitulation of their morphological data is found in Table II.

33. **Uredinopsis Pteridis** D. & H.

Little can be added to the account of the spermogonia of *Uredinopsis Pteridis* already given by Hunter (45) except to say that the literature on *U. Pteridis* and *Peridermium pseudo-balsameum* Arthur and Kern is a maze of confusion (cf. Schmitz, 67; Weir and Hubert, 74; Rhodes, Hedgcock, Bethel and Hartley, 64; Hunter, 45; Kamei, 49).

34. **Peridermium balsameum** Peck

Peck (61) discovered a white-spored rust on the leaves of *Abies balsamea* Mill., which in 1875 he named *Peridermium balsameum.* For many years, as pointed out by Faull (34), this name has been applied to the aecial stage of various North American species of the two genera *Milesia* and *Uredinopsis.* Fraser (38) was the first to demonstrate that five species of *Uredinopsis,* namely, *U. Struthiopteridis, U. Osmundae, U. Atkinsonii, U. Phegopteridis,* and *U. mirabilis* have their aecial stage on *Abies balsamea.* He considered that the peridermia of all of these would pass current for the *P. balsameum* of Peck. The occurrence of these five species on *Abies* was later confirmed by culture experiments carried out under the direction of Professor Faull (34). The Sydows (70) in referring to Fraser's work stated that the peridermia of the various North American species of *Uredinopsis* recorded in their Monographia cannot be distinguished from Peck's *P. balsameum* but they cite *P. balsameum* as a synonym of *U. Struthiopteridis* only. Arthur (15) chose to refer *P. balsameum* to *U. mirabilis;* but he also stated that the aecial stages of *U. Osmundae* and *U. Copelandi* Sydow are similar to those of *U. mirabilis.* Arthur and Kern (17) redescribed *P. balsameum* Peck. Their material comprised numerous specimens, including what they considered Peck's type material from the Adirondack Mts. and without realizing that in it more than one species was involved. Incidentally they ventured the opinion that *Aecidium pseudocolumnare* Kühn, as maintained by Farlow, might be identical with *P. balsameum.*

Faull (34) discovered that three American species of the genus *Milesia* on *Abies balsamea,* as well as those of *Uredinopsis,* occur on the leaves of *Abies balsamea.* Of these, *M. polypodophila* (Bell) Faull,

easily distinguished from the others by the occurrence on leaves 3-8 years old and by its strikingly distinctive morphological characters, apparently had been overlooked by collectors; but the remaining species referred to by him and occurring on leaves of the current season (as do those of the *Uredinopsis* species mentioned), had no doubt passed under the name *P. balsameum*.

It is now known that the genera *Milesia* and *Uredinopsis* in North America, as they occur on *Abies*, can be distinguished from one another by their spermogonia, and that similarly the species *Milesia intermedia* (perhaps more properly named *M. fructuosa* Faull), *M. marginalis* and *M. polypodophila* possess specifically distinctive spermogonia (45). Hence it is now possible to more exactly determine the identity of what Peck himself preserved in his herbarium under the name *Peridermium balsameum*. With this object in view the writer has critically examined Peck's collections stored in the Herbarium of the New York State Museum at Albany, N. Y. and made available through the courtesy of Dr. H. D. House.

The writer found two sheets of exposed specimens and two packets, all ascribed to Professor Peck as collector. There are various later collections in the Herbarium but these are not of pertinent interest here. The first sheet, regarded as the oldest (dating back possibly to 1873), carries several exposed specimens and bears the label, "*Peridermium balsameum* Peck, Adirondack Mts., New York State, July and Aug." Presumably it is the type sheet, though neither it nor any other is so marked. The specimens on this sheet prove to be predominantly *Milesia intermedia;* but one of them is a species of *Uredinopsis*. The second sheet, with several specimens mounted similarly to the first, bears the label, "*Peridermium balsameum* Peck, Charlotteville Swamp, N. Y. State, Aug." It is *M. intermedia*. The third collection was made at N. Elba, N. Y. State, in Aug. 1910, according to the label; it is also *M. intermedia*. The fourth collection is recorded as from L. Avalanche, Adirondacks, N. Y., dated Aug.; but as with the first two sheets, no mention is made of the year. It is a species of *Uredinopsis*.

The writer's conclusions are: (1) Peck's own collections of white-spored peridermial rusts on *Abies* comprised species of both *Milesia* and *Uredinopsis*, and were designated by him as *Peridermium balsameum;* (2) *P. balsameum* cannot accurately be designated as a synonym of any particular species of *Uredinopsis*, as has been done by Sydow and Arthur; (3) what is possibly the type sheet of Peck's *P. balsameum* carries a large proportion of *Milesia intermedia* but some material of an undeterminable species of *Uredinopsis*.

In the study of these plants serial sections were made of selected leaves, and comparisons were made with similar preparations from authentic materials (obtained from controlled cultures) of the various species of *Milesia* and *Uredinopsis* mentioned above, made available through the kindness of Professor Faull.

35. **Aecidium pseudocolumnare** Kühn

The first collections of *Aecidium pseudocolumnare* were made by Kühn in the Black Forest, Germany, in August and September, 1883. The spermogonia were not described but a detailed description of the aecia and aeciospores was given on labels attached to herbarium specimens. The aeciospores were said to be white, finely warted and to measure 18.5–25.7 μ broad and 22.8–37.2 μ long. Winter (76) in 1884 published the description of this *Aecidium* word for word with the description signed by Kühn. Kühn's collections were distributed in Rabenhorst-Winter, Fungi Europaei under the name of *Aecidium pseudocolumnare* J. Kühn, nov. sp. number 3027. It is taken for granted then that this material represents the type for *A. pseudocolumnare*. This name, however, came into general use in Europe as a designation of white-spored peridermia on *Abies alba*. That this has been done uncritically is illustrated by the results of comparative examinations made by the writer of spermogonia from several collections found in the herbaria of the Royal Botanic Gardens, Kew, and the British Museum of Natural History — all regarded as *A. pseudocolumnare*. Aeciospores and peridial cells did not prove sufficiently characteristic to be of diagnostic value. Descriptions of the spermogonia of the various collections follow:

(1) Rabenhorst-Winter, Fungi Europaei no. 3027, *Aecidium pseudocolumnare* J. Kühn, nov. sp. (bearing Kühn's original description). The spermogonia from this collection are subepidermal and measure 160–200 μ broad and 152–180 μ deep. They closely resemble those of *Milesia vogesiaca*.

(2) Krieger, Schädliche Pilze unserer Kulturgewächse no. 74, *Aecidium pseudocolumnare* J. Kühn. The spermogonia are subcuticular and measure 92–140 μ broad and 112–160 μ deep. They most closely resemble those of *Milesia Kriegeriana*.

(3) Krieger, Fungi Saxonici no. 1419, *Aecidium pseudocolumnare* Kühn nov. sp. Very little of this material was available but enough was obtained to show a few subcuticular spermogonia measuring 130–132 μ broad and 92–120 μ deep. They also resemble those of *Milesia Kriegeriana*.

(4) C. E. Broome, *Peridermium columnare* on *Picea Nordmanniana* (*Abies Nordmanniana*), Torquay, ex Herb. M. J. B. Aug. 1867. According to J. Ramsbottom, Keeper of Botany, British Museum of Natural History, this material is originally from the herbarium of Miles Joseph Berkeley. Ten spermogonia from a fragment of the specimen were examined. Nine of these are definitely subcuticular while one is subcuticular only in the center with remains of epidermal cells at the sides overlying the spermogonium. They measure 152–208 μ broad and 140–200 μ deep. The evidence is that the subcuticular spermogonia may belong to either or both *Milesia Polypodii* and *M. Scolopendrii.*

(5) M. C. Cooke, Fungi Britannici exsiccati no. 314, *Peridermium columnare* A. & S., near Torquay, Sept. 1869. E. Parfitt. The spermogonia are deep-seated, subcuticular, measuring 128–180 μ broad and 132–180 μ deep. They also may be referable to either or both *Milesia Polypodii* and *M. Scolopendrii.*

(6) *Aecidium pseudocolumnare* Kühn on *Abies alba.* Kelso, Aug. 1925, Malcolm Wilson. Only a small fragment of an infected needle was examined. The sections were not sufficiently satisfactory to warrant a definite conclusion, since the spermogonia seemed to be distorted. They are deep-seated, large, hemispherical, subcuticular and probably belong to the genus *Milesia.*

(7) *Aecidium pseudocolumnare* Kühn. Powerscourt, Co. Wicklow, P. O'Connor. One collection is dated 11.11.31 and 6.2.31, while a second collection is dated 11.11.31. Although this material was collected late in the year, it is in excellent condition. The peridermia even in the dried state are long and unbroken, and almost every leaf on a branch of considerable size is rusted. For convenience the two collections are referred to respectively as (a) and (b). Two spermogonia examined from (a) are deep-seated, hemispherical and measure 101 μ broad and 168 μ deep. These most closely resemble the spermogonia of *Milesia Kriegeriana.* Four spermogonia from (b) were examined. They are deep-seated, subepidermal, elongate and measure 174–181 μ broad and 181–188 μ deep. They closely resemble spermogonia of the type material of *Aecidium pseudocolumnare.*

A study of the spermogonia in these collections, therefore, clearly indicates that the latter are referable to several distinct species. Hence, just as in North America, until recently, several white-spored rusts on *Abies* have been passing under the name *Peridermium balsameum* Peck, so it would seem that the same is true in Europe for *Aecidium pseudocolumnare.*

III. Subfamily CRONARTIEAE

36. **Cronartium ribicola** Fischer

The spermogonia of *Cronartium ribicola* occur on *Pinus Strobus* L. and other five-needle pines. They are caulicolous, subcortical, forming small blisters. They are located between the outermost layer of cortical cells and the periderm, effuse or indefinite in type. Six spermogonia measured 1.0–3.5 mm. broad and 34–67 μ high. Figure 38 represents a mature spermogonium. Sydow (70) states that the spermogonia are about 2.5 mm. long. Colley's (22) observation that "occasionally long filaments grow some distance out beyond the tips of the spermatiophores" is of especial interest when viewed in the light of recent discoveries in connection with the fusion of spermatia and haploid hyphae. The spermatia according to Colley are pyriform and measure approximately 2.5 × 3.5 μ.

IV. Subfamily CHRYSOMYXEAE

37. **Chrysomyxa Ledi** (A. & S.) DeBary

The spermogonia of *Chrysomyxa Ledi* occur on first year needles of *Picea mariana* (Mill.) B. S. P. and *P. glauca* (Moench) Voss. They are amphigenous, subepidermal and flask-shaped in section (Fig. 37). If the spermogonium happens to form below a stoma the guard cells are carried above the spermogonium. Frequently the epidermal layer, though raised slightly, is left intact; but sometimes the lower walls are attacked and the cells killed. The hypodermal cells within the area of the spermogonium are disrupted, and disappear. The mesophyll cells below the spermogonium are depressed. Twenty-nine spermogonia measured 60–128 μ broad and 45–125 μ high, averaging 105 × 82 μ. The spermatiophores arise from a basal stroma and are directed to a slit-like pore in the epidermis. They are usually one-septate near their bases. The spermatia measure 1.5–2.0 × 3.0–3.5 μ. They are slightly elongate and form catenulately. The pore through which they are emitted measured 4–35 μ broad and 20–80 μ long.

V. Subfamily COLEOSPORIEAE

38. **Coleosporium Helianthi** (Schw.) Arth.

The spermogonia of *Coleosporium Helianthi* are borne on leaves of *Pinus virginiana* Mill. and *P. echinata* Mill. They are numerous, amphigenous and of the applanate, lenticular type; they resemble those of *Hyalopsora Aspidiotus* in shape except that they are elevated more above the surrounding epidermis and do not depress as much the mesophyll cells of the leaf at maturity. The spermogonia form between the mesophyll and the overlying tissues. The latter consist of an

epidermis, a hypodermis and from one to two layers of thick-walled cells irregularly placed under the hypodermis. The spermogonia are most frequently discrete; but they are sometimes confluent. Twelve spermogonia measured 323–458 μ broad and 92–116 μ high, averaging 361 × 103 μ. The spermatiophores are usually single-celled. The spermatia are discharged through a slit 34–92 μ wide. A mature spermogonium showing its relation to the leaf is represented in Fig. 39. In addition to other features, attention should be drawn to long, centrally located hyphae that extend beyond the spermatiophores and the level of the epidermis. These are "flexuous hyphae." Such hyphae may extend as much as 15 μ beyond the epidermal level. When the spermogonia have passed full maturity and the spermatia have been discharged there is no trace left of these hyphae. (cf. Arthur 12, 14, Hedgcock 42, Hedgcock and Hunt 43.)

The materials for the study of this and the other species of *Coleosporium* described below were kindly supplied by Dr. G. G. Hedgcock.

39. **Coleosporium inconspicuum** (Long) Hedgc. & Long

The spermogonia of *Coleosporium inconspicuum* are borne on leaves of *Pinus virginiana* etc. The same general description of form and location applies as for the spermogonia of *C. Helianthi*, except that the spermatiophores are of slightly smaller diameter. Eleven of them measured 226–317 μ broad and 73–85 μ high, averaging 284 × 81 μ.

The immature spermogonium of *C. inconspicuum* depresses the mesophyll cells lying immediately under it; whereas in the mature spermogonium the latter have regained their normal position with the exception that they may be separated by the strands of mycelium. The cells above the young spermogonium (Fig. 40) are raised and flattened; but on either side of the spermogonium they have retained their normal size and position. Differential staining shows that two layers of mesophyll cells immediately under the spermogonium, in contrast with those more distantly located, have in some way been affected by the parasite. (cf. Arthur 14, Hedgcock 42, Hedgcock and Hunt 43.)

40. **Coleosporium Ipomoeae** (Schw.) Burr.

The spermogonia of *Coleosporium Ipomoeae* occur on needles of *Pinus rigida* Mill. etc. They are subepidermal and of the applanate type. They measure 335–490 μ broad and 104–159 μ high. According to Hedgcock (42) they are olivaceous-black to brownish-black, on slightly chlorotic areas. They are amphigenous in *P. rigida* and hypophyllous in *P. echinata*.

41. **Coleosporium delicatulum** (A. & K.) Hedgc. & Long

The spermogonia of *Coleosporium delicatulum* occur on needles of *Pinus rigida* etc. They are amphigenous, subepidermal, applanate, and measure 354 μ broad and 110–122 μ high. According to Hedgcock (42) they are orange chrome to English red on reddened chlorotic areas.

42. **Coleosporium Laciniariae** Arth.

The spermogonia of *Coleosporium Laciniariae* occur on needles of *Pinus rigida* etc. They are discrete, epiphyllous, subepidermal, applanate and measure 323–397 μ broad and 110–122 μ high. According to Hedgcock (42) they are olive to olivaceous-black on yellow chlorotic areas. The spermatiophores usually are one-septate towards their bases.

43. **Coleosporium Solidaginis** (Schw.) Thüm.

The spermogonia of *Coleosporium Solidaginis* are borne on needles of *Pinus rigida* etc. They are usually discrete. They measure 244–366 μ broad and 98–104 μ high. In *P. rigida* they are hypophyllous. According to Hedgcock (42) they are grenadine red on slightly reddened chlorotic areas.

44. **Coleosporium Terebinthinaceae** (Schw.) Arth.

The spermogonia of *Coleosporium Terebinthinaceae* occur on needles of *Pinus virginiana* etc. They are epiphyllous and measure 335–427 μ broad and 80–101 μ high. According to Hedgcock (42) they are "orange rufous to mummy brown, on yellowed chlorotic areas."

45. **Gallowaya pinicola** Arth.

The spermogonia of *Gallowaya pinicola* occur on the leaves of *Pinus virginiana*. They are of the applanate type, lenticular in vertical section, subepidermal and amphigenous. Seven spermogonia measured 244–427 μ broad and 48–92 μ high. Figure 41 represents a mature spermogonium. The spermogonia are nearly always centrally located beneath the guard cells in stomatal cavities and develop between the mesophyll and the epidermis. The underlying mesophyll cells are not usually depressed and the overlying epidermis is very slightly elevated. The contiguous epidermal cells are never flattened as they may be in *Coleosporium* species; but differential staining shows that their lower walls have been affected by the fungus. The stroma is made up of interwoven hyphae overlying the mesophyll cells; from it spermatiophores branch and are arranged periclinally, curving slightly towards a central point under the epidermis. The spermatiophores are attenuate, frequently curved at their tips and usually one-septate, about one-third up from the base. Spermatia do not form.

Arthur (16) places *Gallowaya pinicola* in the genus *Coleosporium*. He states that the spermogonia are rudimentary and not externally visible; Dodge (32) previously described them as vestigial or abortive. Dodge further stated that host tissues above the spermogonia are not fully ruptured and that spermatia are seldom formed. Here we have a parallel case to that of *Calyptospora Goeppertiana*. In *G. pinicola* then, as in *C. Goeppertiana*, the spermogonia cannot function in the way described for *Puccinia* species by Craigie (27).

CONCLUSIONS AND SUMMARY

1. The morphology of the spermogonia of representatives of all the genera, except *Chnoopsora*, of the Melampsoraceae (Dietel, 1928) has been studied in the course of the investigations recorded in this paper.

2. From these studies it is amply demonstrated that spermogonia are of more or less diagnostic value (just as are other organs) in defining or determining species and genera. The features of chief importance in that connection are the form-type, size and position in the host tissues. It should, of course, be recognized that these features can be employed in diagnosis with greater assurance where the complete life history is known and where the spermogonia have been studied and defined from authentic culture material. This may be illustrated by reference to those species of Melampsoraceae whose haploid stages occur on the Pinaceae. In eastern North America the life histories of many of them have been worked out and the spermogonia have been studied from authentic culture material. It so happens that the *aecial* characters of many of these species are not sufficiently distinctive to enable one to recognize the species or in some cases even the genus from haploid material. The *spermogonial* characters, on the other hand, in many such instances have proved to be of diagnostic value and their characters have been incorporated in definitions of the species. It is now possible, therefore, to recognize many of the Melampsoraceae in eastern North America from haploid material alone and without having recourse to cultures. As for western North America, by contrast, little work has been done on life histories of coniferous rusts. An examination of the spermogonia in western collections of coniferous rusts shows that the spermogonia of some of these rusts are surely of diagnostic value; but the delimitation of species is bound to be tentative until life histories are worked out and the exact morphological characters of their spermogonia are incorporated in descriptions of the species. Much the same condition prevails with respect to the European Melampsoraceae.

3. The spermogonia of the Melampsoraceae may be classified according to their form and position in the host tissues, as follows:

A. *Subcuticular* — (a) pustulate — (1) hemispherical to conoidal
(b) immersed — (1) hemispherical; (2) subspherical to spherical

B. *Subepidermal* — (a) applanate
(b) immersed — (1) elliptical; (2) spherical to flask-shaped

C. *Subcortical*

4. Spermogonia have been found for the main part to be characteristic in type for each genus. The one outstanding exception is that of *Melampsora*. In *Melampsora*, as now commonly recognized, two very diverse types of spermogonia are comprised — (1) species in which the spermogonia are robust and deep-seated; (2) species in which the spermogonia are small and pustulate.

Another feature in this connection refers to the importance of giving attention to the spermogonia in surmises as to the genetic position of coniferous rusts where the life histories are unknown. This may be illustrated in such a rust as *Peridermium coloradense*. Certain uredinologists have suggested that it is the haploid stage of a *Melampsorella;* indeed, some have gone so far as to refer it to *Melampsorella Cerastii* (75, 16). An examination of the spermogonia of this rust shows that it cannot possibly be a *Melampsorella*. Its type is that of a *Chrysomyxa*.

5. The spermogonia are of value in establishing or confirming views as to the phylogenetic relationship of genera. An excellent example of this is afforded by the genera *Milesia* and *Uredinopsis*. The similar characters of their spermogonia lend support to the view that these genera are closely related. Another example is afforded by *Pucciniastrum, Thecopsora, Calyptospora* and *Melampsoridium,* in all of which the spermogonia are morphologically similar.

6. Spermogonia have, as indicated above, been found to be of value in the determination of species from haploid material; in some such instances no help is afforded by aecial characters. For example — *Melampsora americana* and *Caeoma Faulliana; Milesia intermedia, M. marginalis* and certain other species of *Milesia* as distinct from one another and from species of *Uredinopsis;* and *Calyptospora Goeppertiana* as distinct from various species of *Pucciniastrum*.

7. Attention is called to the non-spermatia-forming rusts, *Calyptospora Goeppertiana* and *Gallowaya pinicola,* as examples of rusts in which spermatia cannot take part in initiating the diploid phase such as is presumed to be the case for *Puccinia graminis, P. Helianthi* etc.

8. The ontogeny of the spermogonia has been studied more or less completely for the following species — *Melampsora Abieti-Capraearum, M. Larici-Capraearum, Melampsorella Cerastii, Calyptospora Goeppertiana, Hyalopsora Aspidiotus, Milesia intermedia, M. marginalis, M. Kriegeriana, M. Polypodii, Uredinopsis mirabilis, U. Atkinsonii, U. Osmundae* and *Coleosporium inconspicuum.*

The value of the ontogenetical studies of some species lies in the circumstance that it is only in this way that the exact type can be determined. Thus a mature spermogonium may appear to be subcuticular when it is really subepidermal or subepidermal when it is really subcuticular.

9. The spermogonia of the Melampsoraceae lack paraphyses. But "flexuous hyphae," possibly receptive organs, extending beyond the aperture of the spermogonium have been found in numerous species of the Melampsoraceae, namely, *Milesia marginalis, M. polypodophila, M. Kriegeriana, M. Polypodii, M. Scolopendrii, M. vogesiaca, Melampsora Abieti-Capraearum* and *Coleosporium Helianthi.* In *Milesia Scolopendrii* spermatia were occasionally attached to "flexuous hyphae" but the nature of the connection was not determined. "Flexuous hyphae" are greater in diameter for most of their length than spermatiophores and are not so much attenuated.

10. Branching of spermatiophores from the stroma has been demonstrated for *Uredinopsis Atkinsonii* and *Pucciniastrum arcticum.* During the development of the spermogonium the distal ends of the spermatiophores remain free from the overlying epidermis or cuticle. At their maturity the spermatiophores are only about one-half the length of the "flexuous hyphae." The spermatiophores decrease in length as they age. Their cells are always uninucleate. Spermatia are borne catenulately. The "slit" through which spermatia are discharged is, in general, parallel to the long axis of the leaf on which the spermogonium is borne.

11. One new species, *Caeoma Faulliana,* is described in this paper.

12. Morphological data on the spermogonia of the species herein studied are summarized below in tabular form (Table II).

TABLE II

SPERMOGONIA OF MELAMPSORACEAE*

Species	Shape (vertical section)	No. measured	Size (breadth × height in microns) Limits	Average	Remarks
I. SUBFAMILY MELAMPSOREAE					
Melampsora Abieti-Capraearum (M. americana)	Elliptical	67	79–154 × 42–71	99 × 48	Subepidermal, depressed
Melampsora Abieti-Capraearum	Elliptical	54	83–138 × 45–67	110 × 54	Subepidermal, subdepressed
Caeoma Faulliana	Hemispherical to conoidal	45	42–145 × 27–49	80 × 37	Subcuticular, pustulate
Melampsora Abietis-canadensis	Hemispherical flattened to conoidal	34	35–98 × 15–38 (on needles)	66 × 25	Subcuticular, pustular
		77	53–128 × 13–30 (on cones)	78 × 23	
Melampsora Bigelowii	Hemispherical to conoidal	42	50–102 × 15–38	69 × 27	Subcuticular, pustulate
Melampsora Medusae	Hemispherical to conoidal	17	51–105 × 15–30	75 × 23	Subcuticular, pustulate
Melampsora Larici-Capraearum	Hemispherical to conoidal	31	30–101 × 18–38	65 × 38	Subcuticular, pustulate
II. SUBFAMILY PUCCINIASTREAE					
Melampsoridium betulinum	Hemispherical flattened to conoidal	—	45–53 × 12–15	———	Subcuticular, pustulate
Melampsorella Cerastii	Hemispherical flattened	72	99–317 × 27–59	184 × 38	Subcuticular, pustulate
Pucciniastrum Epilobii	Hemispherical flattened	81	45–212 × 16–34	95 × 21	Subcuticular, pustulate
Pucciniastrum Abieti-Chamaenerii	Hemispherical flattened	35	67–196 × 16 -31	102 × 23	Subcuticular, pustulate

Notes: 1. Spermogonia on leaves of current season except as indicated under "Remarks".
2. Spermogonia "amphigenous" except as indicated under "Remarks". The term "amphigenous" is used here if spermogonia have been found on both upper and lower leaf surfaces regardless of whether or not they may usually be restricted to one surface or the other.

TABLE II. (Continued)

Species	Shape (vertical section)	No. measured	Size (breadth × height in microns) Limits	Average	Remarks
II. SUBFAMILY PUCCINIASTREAE. (Continued)					
Pucciniastrum americanum	Hemispherical flattened	29	71–185 × 18–62	124 × 35	Subcuticular, pustulate
Pucciniastrum arcticum	Hemispherical flattened	29	100–167 × 22–51	142 × 32	Subcuticular, pustulate
Thecopsora minima	Hemispherical flattened to conoidal	34	38–120 × 15–25	79 × 20	Subcuticular, pustulate
Thecopsora Myrtilli	Hemispherical to conoidal	15	41–105 × 15-23	72 × 20	Subcuticular, pustulate, hypophyllous
Thecopsora Hydrangeae	Hemispherical flattened to conoidal	35	75–126 × 15–26	99 × 24	Subcuticular, pustulate
Calyptospora Goeppertiana	Hemispherical to conoidal	105	42–137 × 13–30	73 × 21	Subcuticular, pustulate, hypophyllous
Hyalopsora Aspidiotus	Lens-shaped, much flattened	25	311–496 × 86–117	432 × 102	Subepidermal, applanate, hypophyllous On second year needles
Milesia intermedia	Hemispherical to subspherical	53	84–137 × 59–84	110 × 71	Subcuticular, immersed, hypophyllous
Milesia fructuosa	Hemispherical to subspherical	393	72–180 × 40–100	123 × 71	Subcuticular, immersed
Milesia marginalis	Subspherical to almost spherical	50	129–168 × 92–134	147 × 106	Subepidermal, immersed
Milesia polypodophila	Spherical	17	175–234 × 175–243	199 × 212	Subepidermal, immersed, hypophyllous On leaves 3-8 years old
Milesia Blechni	Somewhat flask-shaped	9	110–175 × 105–150	———	Subcuticular, immersed
Milesia Kriegeriana	Hemispherical	16	98–168 × 94–168	129 × 126	Subcuticular, immersed

TABLE II, (Continued)

Species	Shape (vertical section)	No. measured	Size (breadth × height in microns) Limits	Average	Remarks
II. SUBFAMILY PUCCINIASTREAE. (Continued)					
Milesia Polypodii	Hemispherical to slightly flask-shaped	34	120–228 × 105–194	177 × 162	Subcuticular, immersed
Milesia Scolopendrii	Hemispherical to slightly flask-shaped	28	120–228 × 100–188	156 × 140	Subcuticular, immersed
Milesia vogesiaca	Hemispherical to slightly flask-shaped	34	154–241 × 168–214	201 × 195	Subcuticular, immersed
Peridermium rugosum	Spherical	11	144–223 × 144–200	170 × 169	Subepidermal, immersed, hypophyllous On second-year leaves
Uredinopsis mirabilis	Hemispherical	49	58–123 × 35–54	89 × 44	Subcuticular, immersed, hypophyllous
Uredinopsis Atkinsonii	Hemispherical, shallow	65	67–123 × 36–51	96 × 48	Subcuticular, immersed, hypophyllous
Uredinopsis Osmundae	Hemispherical, shallow	72	71–134 × 40–57	104 × 51	Subcuticular, immersed, hypophyllous
Uredinopsis Phegopteridis	Hemispherical, shallow	68	56–125 × 34–58	93 × 48	Subcuticular, immersed, hypophyllous
Uredinopsis Struthiopteridis	Hemispherical, shallow	46	71–129 × 45–58	94 × 50	Subcuticular, immersed, hypophyllous
Uredinopsis Pteridis	Hemispherical, vertically elongated	—	100–159 × 85–110	———	Subcuticular, immersed, hypophyllous On leaves of 1st or 2nd season (?)
Aecidium pseudo-columnare	Subspherical	—	160–200 × 152–180	———	Subepidermal, immersed

TABLE II. (Continued)

Species	Shape (vertical section)	No. measured	Size (breadth × height in microns) Limits	Average	Remarks
III. SUBFAMILY CRONARTIEAE					
Cronartium ribicola	Flattened hemispherical	6	1000–3500 × 34–67	——	Caulicolous, subcortical
IV. SUBFAMILY CHRYSOMYXEAE					
Chrysomyxa Ledi	Flask-shaped	29	60–128 × 45–125	105 × 82	Subepidermal, immersed
V. SUBFAMILY COLEOSPORIEAE					
Coleosporium Helianthi	Lens-shaped, elevated	12	323–458 × 92–116	361 × 103	Subepidermal, applanate
Coleosporium inconspicuum	Lens-shaped, elevated	11	226–317 × 73–85	284 × 81	Subepidermal, applanate, hypophyllous
Coleosporium Ipomoeae	Lens-shaped, elevated	—–	335–490 × 104–159	——	Subepidermal, applanate
Coleosporium delicatulum	Lens-shaped, elevated	—	354– × 110–122	——	Subepidermal, applanate
Coleosporium Laciniariae	Lens-shaped, elevated	—	323–397 × 110–122	——	Subepidermal, applanate, epiphyllous
Colesporium Solidaginis	Lens-shaped, elevated	—	244–366 × 98–104	——	Subepidermal, applanate hypophyllous
Coleosporium Terebinthinaceae	Lens-shaped, elevated	—	335–427 × 80–101	——	Subepidermal, applanate, epiphyllous
Gallowaya pinicola	Lens-shaped, elevated	7	244–427 × 48–92	——	Subepidermal, applanate

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BIBLIOGRAPHY

1. Adams, J. F. (1919). I. Rusts on conifers in Pennsylvania. II. Sexual fusions and development of the sexual organs in the Peridermiums. (Penn. State Coll. Agri. Expt. Sta. Bull. **160**: 3–77.)
2. ——— (1920). The alternate stage of Pucciniastrum Hydrangeae. (Mycologia, **12**: 33–35.)
3. Allen, R. F. (1930). A cytological study of heterothallism in Puccinia graminis. (Jour. Agr. Res. **40**: 585–614.)
4. ——— (1931). Heterothallism in Puccinia triticina. (Science, **74**: 462–463.)
5. ——— (1932). A cytological study of heterothallism in Puccinia triticina. (Jour. Agr. Res. **44**: 733–754.)
6. ——— (1932). A cytological study of heterothallism in Puccinia coronata. (Jour. Agr. Res. **45**: 513–541.)
7. ——— (1933). The spermatia of the corn rust, Puccinia Sorghi. (Phytopath. **23**: 923–925.)
8. ——— (1933). Further cytological studies of heterothallism in Puccinia graminis. (Jour. Agr. Res. **47**: 1–16.)
9. ——— (1933). The spermatia of flax rust. (Phytopath. **23**: 487.)
10. Andrus, C. F. (1931). The mechanism of sex in Uromyces appendiculatus and U. Vignae. (Jour. Agr. Res. **42**: 559–587.)
11. Arthur, J. C. (1904). Taxonomic importance of the spermogonium. Bull. Torr. Bot. Club, **31**: 113–123.)
12. ——— (1907). North American Flora, 7, Part 2.
13. ——— (1910). New species of Uredineae. (VIII) (Bull. Torr. Bot. Club, **37**: 569–580.)
14. ——— (1924). North American Flora, 7, Part 9.
15. ——— (1925). North American Flora, 7, Part 10.
16. ——— (1934). Manual of the rusts in United States and Canada.
17. ——— and D. F. Kern (1906). North American species of Peridermium. (Bull. Torr. Bot. Club, **33**: 403–438.)
18. Bell, H. P. (1924). The rusts of Abies. (Bot. Gaz. **77**: 1–31.)
19. Blackman, V. H. (1904). On the fertilization, alternation of generations and general cytology of the Uredineae. (Ann. Bot. **18**: 323–373.)
20. ——— and H. C. I. Fraser (1906). Further studies on the sexuality of the Uredineae. (Ann. Bot. **20**: 35–48.)
21. Boyce, J. S. (1928). A conspectus of needle rusts on balsam firs in North America. (Phytopath. **18**: 705–708.)
22. Colley, R. H. (1918). Parasitism, morphology and cytology of Cronartium ribicola. (Jour. Agr. Res. **15**: 619–660.)
23. Craigie, J. H. (1927). Experiments on sex in rust fungi. (Nature, **120**: 116–117.)

24. ———— (1927). Discovery of the function of the pycnia of the rust fungi. (Nature, **120**: 765–767.)
25. ———— (1928). On the occurrence of pycnia and aecia in certain rust fungi. (Phytopath. **18**: 1005–1015.)
26. ———— (1931). An experimental investigation of sex in the rust fungi. (Phytopath. **21**: 1001–1040.)
27. ———— (1933). Union of pycniospores and haploid hyphae in Puccinia Helianthi Schw. (Nature, **131**: 25.)
28. DARKER, G. D. (1929). Cultures of Pucciniastrum americanum (Farl.) Arth. and P. arcticum (Lagerh.) Tranz. (Jour. Arnold Arb. **10**: 156–167.)
29. DEBARY, A. (1853). Die Brandpilze, pp. 24–144.
30. ———— (1865). Neue Untersuchungen über die Uredineen, insbesondere die Entwicklung der Puccinia graminis und den Zusammenhang derselben mit Aecidium Berberidis. (Monatsber. K. Preuss. Acad. Wiss. **1865**: 15–49.)
31. ———— (1867). Über den Krebs und die Hexenbesen der Weisstanne. (Bot. Zeit. **25**: 257–264.)
32. DODGE, B. O. (1925). Organization of the telial sorus in the pine rust, Gallowaya pinicola. (Jour. Agr. Res. **31**: 641–651.)
33. FARLOW, W. G. (1885). Notes on some species of Gymnosporangium and Chrysomyxa of the United States. (Proc. Am. Acad. **20**: 322.)
34. FAULL, J. H. (1929). The morphology, biology and phylogeny of the Pucciniastreae. [Proc. Internat. Congr. Plant Sci. Ithaca (1926), **2**: 1735–1745.]
35. ———— (1932). Taxonomy and geographical distribution of the genus Milesia. (Contrib. Arnold Arb. **2**: 1–138.)
36. ———— (1934). The biology of Milesian rusts. (Jour. Arnold Arb. **15**: 50–86.)
37. FRASER, W. P. (1912). Cultures of heteroecious rusts. (Mycologia, **4**: 175–193.)
38. ———— (1913). Further cultures of heteroecious rusts. (Mycologia, **5**: 233–239.)
39. ———— (1914). Notes on Uredinopsis mirabilis and other rusts. (Mycologia, **6**: 25–28.)
40. FROMME, F. D. (1912). Sexual fusions and spore development in the flax rust. (Bull. Torr. Bot. Club, **39**: 113–131.)
41. GUINIER, P. (1931). Note sur deux Pucciniastrum nuisibles aux conifères. (Travaux Cryptog. dédiés à L. Mangin, Museum National d'Hist. Nat. Paris, pp. 373–375.)
42. HEDGCOCK, G. G. (1928). Key to the known aecial forms of Coleosporium occurring in the United States and a list of the host species. (Mycologia, **20**: 97–100.)
43. ———— and N. REX HUNT (1922). Notes on some species of Coleosporium I. (Mycologia, **14**: 244–257.)
44. HERSPERGER, C. (1928). Über das Vorkommen einer Aecidienperidie bei Melampsoren. (Mitt. Nat. Ges. Bern.)
45. HUNTER, L. M. (1927). Comparative study of spermogonia of rusts of Abies. (Bot. Gaz. **83**: 1–23.)
46. ———— (1935). A preliminary note on life history studies of European species of Milesia. (Jour. Arnold Arb. **16**: 143.)
47. JACKSON, H. S. (1931). The rusts of South America based on the Holway collections III. (Mycologia, **23**: 96–117.)
48. ———— (1931). The rusts of South America based on the Holway collections IV. (Mycologia, **23**: 332–364.)

49. Kamei, S. (1930). On the life history of Uredinopsis Pteridis with a special bearing on its peridermial stage. (Ann. Phytopath. Soc. Jap. **2**: 1–22.)
50. ——— (1932). Notes on the cultural study of a new species of Hyalopsora. (Trans. Sapporo Nat. Hist. Soc. **12**: 27–34.)
51. Klebahn, H. (1899). Kulturversuche mit heteröcischen Rostpilzen. (Zeitsch. Pflanzenkr. **9**: 14–26.)
52. ——— (1916). Kulturversuche mit Rostpilzen. (Zeitsch. Pflanzenkr. **26**: 257–277.)
53. Lepik, E. (1928). Differential staining of Peronosporaceae. (Phytopath. **18**: 869–872.)
54. Ludwig, C. A. (1915). Notes on some North American rusts with Caeoma-like sori. (Phytopath. **5**: 273–284.)
55. Maire, R. (1900). L'évolution nucléaire chez les Endophyllum. (Jour. de Bot. **14**: 80–92.)
56. Mayor, E. (1919–1921). Etude expérimentale de Melampsora Abieti-Capraearum Tubeuf. (Bull. Soc. Mycol. **36**: 191–203.)
57. ——— (1922). Etude expérimentale d'Urédinées hétéroiques. (Bull. Soc. Neuchât. Sci. Nat. **47**: 67–73.)
58. ——— (1933). Notes mycologiques VIII. (Bull. Soc. Neuchât. Sci. Nat. **58**: 23–26.)
59. Meyen, F. J. F. (1841). Pflanzen-Pathologie, pp. 141–150.
60. Neuman, R. (1894). Ueber die Entwickelungsgeschichte der Aecidien und Spermogonien der Uredineen. (Hedwigia, **33**: 346–361.)
61. Peck, C. (1875). Rep. N. Y. State Mus. **27**: 104.
62. Pierson, R. K. (1933). Fusion of pycniospores with filamentous hyphae in the white pine blister rust. (Nature, **131**: 728–729.)
63. Plowright, C. B. (1891). Einige Impfversuche mit Rostpilzen. (Zeitsch. Pflanzenkr. **1**: 130–131.)
64. Rhoads, A. S., G. G. Hedgcock, E. Bethel and C. Hartley (1918). Host relationships of the North American rusts, other than Gymnosporangiums, which attack conifers. (Phytopath. **8**: 309–352.)
65. Rosen, F. (1893). Beiträge zur Kenntniss der Pflanzenzellen. (Cohn's Beiträge zur Biologie der Pflanzen, **6**: 237–266.)
66. Sappin-Trouffy, M. (1896). Recherches histologiques sur la famille des Urédinées. (Le Botaniste, **5**: 59–244.)
67. Schmitz, H. (1916). Preliminary note on the occurrence of Peridermium balsameum in Washington. (Phytopath. **6**: 369–371.)
68. Spaulding, P. (1911). Rusts of Tsuga canadensis. (Science, **33**: 194.)
69. ——— (1911). The rusts of Tsuga canadensis. (Phytopath. **1**: 94–96.)
70. Sydow, P. and H. (1915). Monographia Uredinearum, III.
71. Thümen, F. (1880). Die Blasenrost-Pilze der Coniferen. (Mitteil. Forstl. Versuchswesen Oesterreichs, II. 320.)
72. Tulasne, L. R. (1854). Second mémoire sur les Urédinées et les Ustilaginées. (Ann. Sci. Nat. Bot. Sér. 4. **2**: 77–196.)
73. Unger, F. (1833). Die Exantheme der Pflanzen und einige mit diesen verwandten Krankheiten der Gewächse, pp. 297–301.)
74. Weir, J. R. and E. E. Hubert (1917). Observations on forest tree rusts. (Amer. Jour. Bot. **4**: 327–335.)
75. ——— ——— (1918). Notes on forest tree rusts. (Phytopath. **8**: 114–118.)
76. Winter, G. (1884). Repertorium Rabenhorstii fungi europaei et extraeuropaei. Cent. XXXI et XXXII cura Dr. G. Winter. (Hedwigia, **23**: 169.)

EXPLANATION OF PLATES

PLATE 182

Fig. 1. Lateral vertical section of mature spermogonium of *Melampsora Abieti-Capraearum* from longitudinal section of leaf of *Abies balsamea*. × 700.

Fig. 2. Median vertical section of an immature spermogonium of *Melampsora Abieti-Capraearum* located under guard cell in longitudinal section of leaf of *A. balsamea*. × 480. Note the branched spermatiophores.

Fig. 3. Median vertical section of an immature spermogonium of *Melampsora Abieti-Capraearum,* approximately 2/3 mature size, from transverse section of leaf of *A. balsamea*. × 212. Dark areas within spermogonium are remains of mesophyll cells.

Fig. 4. Median vertical section of the mature spermogonium of *Caeoma Faulliana* from a transverse section of leaf of *Abies lasiocarpa*. × 135.

Fig. 5. Median vertical section of mature spermogonium of *Melampsoridium betulinum* from transverse section of leaf of *Larix decidua*. × 280.

Fig. 6. Median vertical section of mature spermogonium of *Melampsora Abietis-canadensis* from cone scale of *Tsuga canadensis*. × 325.

Fig. 7. Median vertical section of mature spermogonium of *Melampsora Bigelowii* from longitudinal section of leaf of *Larix laricina*. × 280. Note mass of spermatia above spermogonium.

Fig. 8. Median vertical section of immature spermogonium of *Melampsora Larici-Capraearum* from transverse section of leaf of *Larix laricina*. × 330. Note unbroken elevated cuticle.

Fig. 9. Median vertical section of mature spermogonia of *Melampsora Larici-Capraearum* from transverse section of leaf of *Larix decidua*. × 280.

PLATE 183

Fig. 10. Median vertical section of a mature spermogonium of *Melampsorella Cerastii* from longitudinal section of leaf of *A. balsamea*. × 560. Note cuticle ruptured at right overlying spermogonium.

Fig. 11. Median vertical section of immature spermogonium of *Calyptospora Goeppertiana* from transverse section of leaf of *A. balsamea*. × 413.

Fig. 12. Median vertical section of mature spermogonium of *Pucciniastrum arcticum* from transverse section of leaf of *Picea glauca*. × 280.

Fig. 13. Median vertical section of mature spermogonium of *Pucciniastrum arcticum* from transverse section of leaf of *Picea glauca*. × 625. Note cells in stroma from which spermatiophores branch.

Fig. 14. Median vertical section of spermogonium of *Thecopsora Myrtilli* from transverse section of leaf of *Tsuga canadensis*. × 280.

Fig. 15. Transverse section of leaf of *A. balsamea* infected with *Hyalopsora Aspidiotus*. Note abundance of mycelium in intercellular spaces, spermogonia and spermatia strewn over leaf surface. × 90.

PLATE 184

Fig. 16. Median vertical section of spermogonium of *Hyalopsora Aspidiotus* at very early stage in development, from longitudinal section of leaf of *A. balsamea*. × 290.

Fig. 17. Median vertical section of immature spermogonium of *Milesia intermedia* from transverse section of leaf of *A. balsamea*. × 288. Note depressed epidermal cells, spermatiophores and spermatia and overlying unruptured cuticle, with intermediate layer, darkly stained, beneath.

Fig. 18. Median vertical section of immature spermogonium of *Milesia intermedia* from transverse section of leaf of *A. balsamea*. × 888. Note depressed epidermal cells, separated spermatiophores, spermatia and cuticle minus intermediate layer in centre above spermogonium.

Fig. 19. Median vertical section of very early stage in the development of the spermogonium of *Milesia marginalis* from transverse section of leaf of *A. balsamea*. × 550. Note central cell in epidermis has been invaded.

Fig. 20. Median vertical section of early stage in the development of the spermogonium of *Milesia marginalis* from longitudinal section of *A. balsamea*. × 666. Note depressed mesophyll cells, spermatiophores and central epidermal cell invaded by enlarged hyphae.

PLATE 185

Fig. 21. Median vertical section of young spermogonium — a later stage than that shown in Fig. 23 — of *Milesia marginalis* from transverse section of leaf of *A. balsamea*. × 374. Note epidermal cells have disappeared.

Fig. 22. Median vertical section of spermogonium of *Milesia marginalis*, epidermal cells over left, from transverse section of leaf of *A. balsamea*. × 280.

Fig. 23. Median vertical section of mature spermogonium of *Milesia marginalis* from transverse section of leaf of *A. balsamea*. × 280. Note teeth from outer epidermal wall projecting into spermogonium.

Fig. 24. Median vertical section of mature spermogonium of *Milesia polypodophila* from transverse section of leaf of *A. balsamea*. × 280. Note two "flexuous hyphae."

Fig. 25. Median vertical section of an immature spermogonium of *Milesia Polypodii*, showing an early stage of development, from transverse section of leaf of *Abies concolor*. × 280. Note epidermal cells below.

Fig. 26. Median vertical section of mature spermogonium of *Milesia polypodophila* from transverse section of leaf of *A. balsamea*. × 280. Note shortened spermatiophores and chains of spermatia.

Fig. 27. *Milesia Scolopendrii*, "flexuous hypha" with spermatia attached. × 1000. This is a higher magnification of Fig. 28.

PLATE 186

Figs. 28 and 29. Photographs of median vertical section of mature spermogonium of *Milesia Scolopendrii* from transverse section of mature leaf of *A. concolor* from hand section, each taken at a different focus. Note flexuous hyphae with spermatia attached.

Fig. 30. Median vertical section of mature spermogonium of *Milesia Blechni* from transverse section of leaf of *Abies alba*. × 300.
Fig. 31. Median vertical section of mature spermogonium of *Milesia Kriegeriana* from transverse section of leaf of *A. alba*. × 300.
Fig. 32. Median vertical section of immature spermogonium of *Milesia Polypodii*, 2/3 mature size, from transverse section of leaf of *A. concolor*. × 372. Note short spermatiophores and central core of long hyphae.
Fig. 33. Mature spermogonium of *Milesia Polypodii* from transverse section of leaf of *A. alba*. × 280. Note "flexuous hyphae" in central cavity.

PLATE 187

Fig. 34. Median vertical section of mature spermogonium of *Milesia vogesiaca*, from transverse section of leaf of *A. alba*. × 300.
Fig. 35. Median vertical section of immature spermogonium of *Uredinopsis mirabilis*, from transverse section of leaf of *A. balsamea*. × 446.
Fig. 36. Median vertical section of mature spermogonium of *Uredinopsis Atkinsonii*, from transverse section of leaf of *A. balsamea* to show branching of spermatiophores from stroma. × 420.
Fig. 37. Median vertical section of mature spermogonium of *Chrysomyxa Ledi*, from transverse section of leaf of *Picea mariana*. × 350.

PLATE 188

Fig. 38. Median vertical section of mature spermogonium of *Cronartium ribicola* from stem of *Pinus Strobus*. × 170.
Fig. 39. Median vertical section of mature spermogonium of *Coleosporium Helianthi*, from transverse section of leaf of *Pinus virginiana*. × 170.
Fig. 40. Median vertical section of immature spermogonium of *Coleosporium inconspicuum*, from longitudinal section of leaf of *P. virginiana*. × 170.
Fig. 41. Median vertical section of spermogonium of *Gallowaya pinicola* from transverse section of leaf of *P. virginiana*. × 142.

LABORATORY OF PLANT PATHOLOGY,
ARNOLD ARBORETUM, HARVARD UNIVERSITY.